THE PROBLEMS OF HEREDITY AND THEIR SOLUTION*

An exact determination of the laws of heredity will probably work more change in man's outlook on the world, and in his power over nature, than any other advance in natural knowledge that can be clearly foreseen.

There is no doubt whatever that these laws can be determined. In comparison with the labour that has been needed for other great discoveries we may even expect that the necessary effort will be small. It is rather remarkable that while in other branches of physiology such great progress has of late been made, our knowledge of the phenomena of heredity has increased but little; though that these phenomena constitute the basis of all evolutionary science and the very central problem of natural history is admitted by all. Nor is this due to the special difficulty of such inquiries so much as to general neglect of the subject.

* The first half of this paper is reprinted with additions and modifications from the *Journal of the Royal Horticultural Society*, 1900, vol. xxv., parts 1 and 2. Written almost immediately after the rediscovery of Mendel, it will be seen to be already in some measure out of date, but it may thus serve to show the relation of the new conceptions to the old.

It is in the hope of inducing others to follow these lines of investigation that I take the problems of heredity as the subject of this lecture to the Royal Horticultural Society.

No one has better opportunities of pursuing such work than horticulturists and stock breeders. They are daily witnesses of the phenomena of heredity. Their success also depends largely on a knowledge of its laws, and obviously every increase in that knowledge is of direct and special importance to them.

The want of systematic study of heredity is due chiefly to misapprehension. It is supposed that such work requires a lifetime. But though for adequate study of the complex phenomena of inheritance long periods of time must be necessary, yet in our present state of deep ignorance almost of the outline of the facts, observations carefully planned and faithfully carried out for even a few years may produce results of great value. In fact, by far the most appreciable and definite additions to our knowledge of these matters have been thus obtained.

There is besides some misapprehension as to the kind of knowledge which is especially wanted at this time, and as to the modes by which we may expect to obtain it. The present paper is written in the hope that it may in some degree help to clear the ground of these difficulties by a preliminary consideration of the question, How far have we got towards an exact knowledge of heredity, and how can we get further?

Now this is pre-eminently a subject in which we must distinguish what we *can* do from what we want to do. We *want* to know the whole truth of the matter; we want to know the physical basis, the inward and essential nature, "the causes," as they are sometimes called, of heredity: but we want also to know the laws which the outward and visible phenomena obey.

Let us recognise from the outset that as to the essential nature of these phenomena we still know absolutely nothing. We have no glimmering of an idea as to what constitutes the essential process by which the likeness of the parent is transmitted to the offspring. We can study the processes of fertilisation and development in the finest detail which the microscope manifests to us, and we may fairly say that we have now a considerable grasp of the visible phenomena; but of the nature of the physical basis of heredity we have no conception at all. No one has yet any suggestion, working hypothesis, or mental picture that has thus far helped in the slightest degree to penetrate beyond what we see. The process is as utterly mysterious to us as a flash of lightning is to a savage. We do not know what is the essential agent in the transmission of parental characters, not even whether it is a material agent or not. Not only is our ignorance complete, but no one has the remotest idea how to set to work on that part of the problem. We are in the state in which the students of physical science were, in the period when it was open to anyone to believe that heat was a material substance or not, as he chose.

But apart from any conception of the essential modes of transmission of characters, we *can* study the outward facts of the transmission. Here, if our knowledge is still very vague, we are at least beginning to see how we ought to go to work. Formerly naturalists were content with the collection of numbers of isolated instances of transmission—more especially, striking and peculiar cases—the sudden appearance of highly prepotent forms, and the like. We are now passing out of that stage. It is not that the interest of particular cases has in any way diminished—for such records will always have their value—but it has become likely that general expressions will be found capable of sufficiently wide application to be justly called "laws" of heredity. That this is so was till recently due almost entirely to the work of Mr F. Galton, to whom we are indebted for the first systematic attempt to enuntiate such a law.

All laws of heredity so far propounded are of a statistical character and have been obtained by statistical methods. If we consider for a moment what is actually meant by a "law of heredity" we shall see at once why these investigations must follow statistical methods. For a "law" of heredity is simply an attempt to declare the course of heredity under given conditions. But if we attempt to predicate the course of heredity we have to deal with conditions and groups of causes wholly unknown to us, whose presence we cannot recognize, and whose magnitude we cannot estimate in any particular case. The course of heredity in particular cases therefore cannot be foreseen.

Of the many factors which determine the degree to which a given character shall be present in a given individual only one is usually known to us, namely, the degree to which that character is present in the parents. It is common knowledge that there is not that close correspondence between parent and offspring which would result were this factor the only one operating; but that, on the contrary, the resemblance between the two is only an uncertain one.

In dealing with phenomena of this class the study of single instances reveals no regularity. It is only by collection of facts in great numbers, and by statistical treatment of the mass, that any order or law can be perceived. In the case of a chemical reaction, for instance, by suitable means the conditions can be accurately reproduced, so that in every individual case we can predict with certainty that the same result will occur. But with heredity it is somewhat as it is in the case of the rainfall. No one can say how much rain will fall to-morrow in a given place, but we can predict with moderate accuracy how much will fall next year, and for a period of years a prediction can be made which accords very closely with the truth.

Similar predictions can from statistical data be made as to the duration of life and a great variety of events, the conditioning causes of which are very imperfectly understood. It is predictions of this kind that the study of heredity is beginning to make possible, and in that sense laws of heredity can be perceived.

We are as far as ever from knowing *why* some characters are transmitted, while others are not; nor can anyone yet foretell which individual parent will transmit characters to the offspring, and which will not; nevertheless the progress made is distinct.

As yet investigations of this kind have been made in only a few instances, the most notable being those of Galton on human stature, and on the transmission of colours in Basset hounds. In each of these cases he has shown that the expectation of inheritance is such that a simple arithmetical rule is approximately followed. The rule thus arrived at is that of the whole heritage of the offspring the two parents together on an average contribute one half, the four grandparents one-quarter, the eight great-grandparents one-eighth, and so on, the remainder being contributed by the remoter ancestors.

Such a law is obviously of practical importance. In any case to which it applies we ought thus to be able to predict the degree with which the purity of a strain may be increased by selection in each successive generation.

To take a perhaps impossibly crude example, if a seedling show any particular character which it is desired to fix, on the assumption that successive self-fertilisations are possible, according to Galton's law the expectation of purity should be in the first generation of self-fertilisation 1 in 2, in the second generation 3 in 4, in the third 7 in 8, and so on*.

But already many cases are known to which the rule in any simple form will not apply. Galton points out that it takes no account of individual prepotencies. There are, besides, numerous cases in which on crossing two varieties the character of one variety almost always appears in each member of the first cross-bred generation. Examples of these will be familiar to those who have experience in such matters. The offspring of the Polled Angus cow and the Shorthorn bull is almost invariably polled or with very small loose "scurs." Seedlings raised by crossing *Atropa belladonna* with the yellow-fruited variety have without exception the blackish-purple fruits of the type. In several hairy species when a cross with a glabrous variety is made, the first cross-bred generation is altogether hairy†.

Still more numerous are examples in which the characters of one variety very largely, though not exclusively, predominate in the offspring.

* See later. Galton gave a simple diagrammatic representation of his law in *Nature*, 1898, vol. LVII. p. 293.

† These we now recognize as examples of Mendelian 'dominance.'

These large classes of exceptions—to go no further—indicate that, as we might in any case expect, the principle is not of universal application, and will need various modifications if it is to be extended to more complex cases of inheritance of varietal characters. No more useful work can be imagined than a systematic determination of the precise "law of heredity" in numbers of particular cases.

Until lately the work which Galton accomplished stood almost alone in this field, but quite recently remarkable additions to our knowledge of these questions have been made. In the year 1900 Professor de Vries published a brief account* of experiments which he has for several years been carrying on, giving results of the highest value.

The description is very short, and there are several points as to which more precise information is necessary both as to details of procedure and as to statement of results. Nevertheless it is impossible to doubt that the work as a whole constitutes a marked step forward, and the full publication which is promised will be awaited with great interest.

The work relates to the course of heredity in cases where definite varieties differing from each other in some *one* definite character are crossed together. The cases are all examples of discontinuous variation: that is to say, cases in which actual intermediates between the parent forms are not usually produced on crossing†. It is shown that the subsequent posterity obtained by self-fertilising these cross-breds or hybrids, or by breeding them with each other, break up into the original parent forms according to fixed numerical rule.

* *Comptes Rendus*, March 26, 1900, and *Ber. d. Deutsch. Bot. Ges.* xviii. 1900, p. 83.

† This conception of discontinuity is of course pre-Mendelian.

Professor de Vries begins by reference to a remarkable memoir by Gregor Mendel*, giving the results of his experiments in crossing varieties of *Pisum sativum*. These experiments of Mendel's were carried out on a large scale, his account of them is excellent and complete, and the principles which he was able to deduce from them will certainly play a conspicuous part in all future discussions of evolutionary problems. It is not a little remarkable that Mendel's work should have escaped notice, and been so long forgotten.

For the purposes of his experiments Mendel selected seven pairs of characters as follows:—

1. Shape of ripe seed, whether round; or angular and wrinkled.

2. Colour of "endosperm" (cotyledons), whether some shade of yellow; or a more or less intense green.

3. Colour of the seed-skin, whether various shades of grey and grey-brown; or white.

4. Shape of seed-pod, whether simply inflated; or *deeply constricted between the seeds.*

5. Colour of unripe pod, whether a shade of green; or bright yellow.

6. Nature of inflorescence, whether the flowers are arranged along the axis of the plant; or are terminal and form a kind of umbel.

7. Length of stem, whether about 6 or 7 ft. long, or about $\frac{3}{4}$ to $1\frac{1}{2}$ ft.

Large numbers of crosses were made between Peas differing *in respect of one of each of these pairs of characters.*

* 'Versuche üb. Pflanzenhybriden' in the *Verh. d. Naturf. Ver. Brünn*, iv. 1865.

It was found that in each case the offspring of the cross exhibited the character of one of the parents in almost undiminished intensity, and intermediates which could not be at once referred to one or other of the parental forms were not found.

In the case of each pair of characters there is thus one which in the first cross prevails to the exclusion of the other. This prevailing character Mendel calls the *dominant* character, the other being the *recessive* character*.

That the existence of such "dominant" and "recessive" characters is a frequent phenomenon in cross-breeding, is well known to all who have attended to these subjects.

By letting the cross-breds fertilise themselves Mendel next raised another generation. In this generation were individuals which showed the dominant character, but also individuals which presented the recessive character. Such a fact also was known in a good many instances. But Mendel discovered that in this generation the numerical proportion of dominants to recessives is on an average of cases approximately constant, being in fact *as three to one.* With very considerable regularity these numbers were approached in the case of each of his pairs of characters.

There are thus in the first generation raised from the cross-breds 75 per cent. dominants and 25 per cent. recessives.

These plants were again self-fertilised, and the offspring of each plant separately sown. It next appeared that the offspring of the recessives *remained pure recessive,* and in subsequent generations never produced the dominant again.

But when the seeds obtained by self-fertilising the

* Note that by these novel terms the complications involved by use of the expression "prepotent" are avoided.

dominants were examined and sown it was found that the dominants were not all alike, but consisted of two classes, (1) those which gave rise to pure dominants, and (2) others which gave a mixed offspring, composed partly of recessives, partly of dominants. Here also it was found that the average numerical proportions were constant, those with pure dominant offspring being to those with mixed offspring as one to two. Hence it is seen that the 75 per cent. dominants are not really of similar constitution, but consist of twenty-five which are pure dominants and fifty which are really cross-breds, though, like the cross-breds raised by crossing the two original varieties, they only exhibit the dominant character.

To resume, then, it was found that by self-fertilising the original cross-breds the same proportion was always approached, namely—

25 dominants, 50 cross-breds, 25 recessives,
or $1D : 2DR : 1R$.

Like the pure recessives, the pure dominants are thenceforth pure, and only give rise to dominants in all succeeding generations studied.

On the contrary the fifty cross-breds, as stated above, have mixed offspring. But these offspring, again, in their numerical proportions, follow the same law, namely, that there are three dominants to one recessive. The recessives are pure like those of the last generation, but the dominants can, by further self-fertilisation, and examination or cultivation of the seeds produced, be again shown to be made up of pure dominants and cross-breds in the same proportion of one dominant to two cross-breds.

The process of breaking up into the parent forms is thus continued in each successive generation, the same numerical law being followed so far as has yet been observed.

Mendel made further experiments with *Pisum sativum*, crossing pairs of varieties which differed from each other in *two* characters, and the results, though necessarily much more complex, showed that the law exhibited in the simpler case of pairs differing in respect of one character operated here also.

In the case of the union of varieties AB and ab differing in two distinct pairs of characters, A and a, B and b, of which A and B are dominant, a and b recessive, Mendel found that in the first cross-bred generation there was only *one* class of offspring, really $AaBb$.

But by reason of the dominance of one character of each pair these first crosses were hardly if at all distinguishable from AB.

By letting these $AaBb$'s fertilise themselves, only *four* classes of offspring seemed to be produced, namely,

AB	showing	both dominant characters.
Ab	,,	dominant A and recessive b.
aB	,,	recessive a and dominant B.
ab	,,	both recessive characters a and b.

The numerical ratio in which these classes appeared were also regular and approached the ratio

$$9AB : 3Ab : 3aB : 1ab.$$

But on cultivating these plants and allowing them to fertilise themselves it was found that the members of the

Ratios		
1		ab class produce only ab's.
3	$\begin{cases}1\\2\end{cases}$	aB class may produce either all aB's, *or* both aB's and ab's.

RATIOS

3	1	*Ab* class may produce either all *Ab*'s,
	2	*or* both *Ab*'s and *ab*'s.
9	1	*AB* class may produce either all *AB*'s,
	2	*or* both *AB*'s and *Ab*'s,
	2	*or* both *AB*'s and *aB*'s,
	4	*or* all four possible classes again, namely, *AB*'s, *Ab*'s, *aB*'s, and *ab*'s,

and the average number of members of each class will approach the ratio 1 : 3 : 3 : 9 as indicated above.

The details of these experiments and of others like them made with *three* pairs of differentiating characters are all set out in Mendel's memoir.

Professor de Vries has worked at the same problem in some dozen species belonging to several genera, using pairs of varieties characterised by a great number of characters: for instance, colour of flowers, stems, or fruits, hairiness, length of style, and so forth. He states that in all these cases Mendel's principles are followed.

The numbers with which Mendel worked, though large, were not large enough to give really smooth results*; but with a few rather marked exceptions the observations are remarkably consistent, and the approximation to the numbers demanded by the law is greatest in those cases where the largest numbers were used. When we consider, besides, that Tschermak and Correns announce definite confirmation in the case of *Pisum*, and de Vries adds the evidence of his long series of observations on other species and orders, there can be no doubt that Mendel's law is a substantial

* Professor Weldon (p. 232) takes great exception to this statement, which he considerately attributes to "some writers." After examining the conclusions he obtained by algebraical study of Mendel's figures I am disposed to think my statement not very far out.

reality; though whether some of the cases that depart most widely from it can be brought within the terms of the same principle or not, can only be decided by further experiments.

One may naturally ask, How can these results be brought into harmony with the facts of hybridisation hitherto known; and, if all this is true, how is it that others who have carefully studied the phenomena of hybridisation have not long ago perceived this law? The answer to this question is given by Mendel at some length, and it is, I think, satisfactory. He admits from the first that there are undoubtedly cases of hybrids and cross-breds which maintain themselves pure and do not break up. Such examples are plainly outside the scope of his law. Next he points out, what to anyone who has rightly comprehended the nature of discontinuity in variation is well known, that the variations in *each* character must be *separately* regarded. In most experiments in crossing, forms are taken which differ from each other in a multitude of characters—some continuous, others discontinuous, some capable of blending with their contraries, while others are not. The observer on attempting to perceive any regularity is confused by the complications thus introduced. Mendel's law, as he fairly says, could only appear in such cases by the use of overwhelming numbers, which are beyond the possibilities of practical experiment. Lastly, no previous observer had applied a strict statistical method.

Both these answers should be acceptable to those who have studied the facts of variation and have appreciated the nature of Species in the light of those facts. That different species should follow different laws, and that the same law should not apply to all characters alike, is exactly what we have every right to expect. It will also be remembered that the principle is only explicitly declared to apply to discontinuous characters*. As stated also it can only be true where reciprocal crossings lead to the same result. Moreover, it can only be tested when there is no sensible diminution in fertility on crossing.

Upon the appearance of de Vries' paper announcing the "rediscovery" and confirmation of Mendel's law and its extension to a great number of cases two other observers came forward almost simultaneously and independently described series of experiments fully confirming Mendel's work. Of these papers the first is that of Correns, who repeated Mendel's original experiment with Peas having seeds of different colours. The second is a long and very valuable memoir of Tschermak, which gives an account of elaborate researches into the results of crossing a number of varieties of *Pisum sativum.* These experiments were in many cases carried out on a large scale, and prove the main fact enuntiated by Mendel beyond any possibility of contradiction. The more exhaustive of these researches are those of Tschermak on Peas and Correns on several varieties of Maize. Both these elaborate investigations have abundantly proved the general applicability of Mendel's law to the character of the plants studied, though both indicate some few exceptions. The details of de Vries' experiments are promised in the second volume of his most valuable *Mutationstheorie.* Correns in regard to Maize and Tschermak in the case of *P. sativum* have obtained further proof that Mendel's law holds as well in the case of varieties differing from each other in *two* pairs of characters, one of each pair being dominant, though of course a more complicated expression is needed in such cases†.

* See later.

† Tschermak's investigations were besides directed to a re-exami-

That we are in the presence of a new principle of the highest importance is manifest. To what further conclusions it may lead us cannot yet be foretold. But both Mendel and the authors who have followed him lay stress on one conclusion, which will at once suggest itself to anyone who reflects on the facts. For it will be seen that the results are such as we might expect if it be imagined that the cross-bred plant produced pollen grains and egg-cells, each of which bears only *one* of the alternative varietal characters and not both. If this were so, and if on an average the same number of pollen grains and egg-cells transmit each of the two characters, it is clear that on a random assortment of pollen grains and egg-cells Mendel's law would be obeyed. For 25 per cent. of "dominant" pollen grains would unite with 25 per cent. "dominant" egg-cells; 25 per cent. "recessive" pollen grains would similarly unite with 25 per cent. "recessive" egg-cells; while the remaining 50 per cent. of each kind would unite together. It is this consideration which leads both Mendel and those who have followed him to assert that these facts of crossing prove that each egg-cell and each pollen grain is pure in respect of each character to which the law applies. It is highly desirable that varieties differing in the form of their pollen should be made the subject of these experiments, for it is quite possible that in such a case strong confirmation of this deduction might be obtained. [Preliminary trials made with reference to this point have so far given negative results. Remembering that a pollen grain is not a germ-cell, but only a bearer of

nation of the question of the absence of beneficial results on cross-fertilising *P. sativum*, a subject already much investigated by Darwin, and upon this matter also important further evidence is given in great detail.

a germ-cell, the hope of seeing pollen grains differentiated according to the characters they bear is probably remote. Better hopes may perhaps be entertained in regard to spermatozoa, or possibly female cells.]

As an objection to the deduction of purity of germ-cells, however, it is to be noted that though true intermediates did not generally occur, yet the intensity in which the characters appeared did vary in degree, and it is not easy to see how the hypothesis of *perfect* purity in the reproductive cells can be supported in such cases. Be this, however, as it may, there is no doubt we are beginning to get new lights of a most valuable kind on the nature of heredity and the laws which it obeys. It is to be hoped that these indications will be at once followed up by independent workers. Enough has been said to show how necessary it is that the subjects of experiment should be chosen in such a way as to bring the laws of heredity to a real test. For this purpose the first essential is that the differentiating characters should be few, and that all avoidable complications should be got rid of. Each experiment should be reduced to its simplest possible limits. The results obtained by Galton, and also the new ones especially described in this paper, have each been reached by restricting the range of observation to one character or group of characters, and it is certain that by similar treatment our knowledge of heredity may be rapidly extended.

To the above popular presentation of the essential facts, made for an audience not strictly scientific, some addition, however brief, is called for. First, in regard to the law of Ancestry, spoken of on p. 5. Those who are acquainted with Pearson's *Grammar of Science*, 2nd ed. published early in

1900, the same author's paper in *Proc. R. S.* vol. 66, 1900, p. 140, or the extensive memoir (pubd. Oct. 1900), on the inheritance of coat-colour in horses and eye-colour in man (*Phil. Trans.* 195, A, 1900, p. 79), will not need to be told that the few words I have given above constitute a most imperfect diagram of the operations of that law as now developed. Until the appearance of these treatises it was, I believe, generally considered that the law of Ancestral Heredity was to be taken as applying to phenomena like these (coat-colour, eye-colour, &c.) where the inheritance is generally *alternative*, as well as to the phenomena of *blended* inheritance.

Pearson, in the writings referred to, besides withdrawing other large categories of phenomena from the scope of its operations, points out that the law of Ancestral Heredity does not satisfactorily express the cases of alternative inheritance. He urges, and with reason, that these classes of phenomena should be separately dealt with.

The whole issue as regards the various possibilities of heredity now recognized will be made clearer by a very brief exposition of the several conceptions involved.

If an organism producing germ-cells of a given constitution, uniform in respect of the characters they bear, breeds with another organism* bearing *precisely similar* germ-cells, the offspring resulting will, if the conditions are identical, be uniform.

In practice such a phenomenon is seen in *pure*-breeding. It is true that we know no case in nature where all the germ-cells are thus identical, and where no variation takes place beyond what we can attribute to conditions, but we

* For simplicity the case of self-fertilisation is omitted from this consideration.

know many cases where such a result is approached, and very many where all the essential features which we regard as constituting the characters of the breed are reproduced with approximate certainty in every member of the pure-bred race, which thus closely approach to uniformity.

But if two germ-cells of dissimilar constitution unite in fertilisation, what offspring are we to expect*? First let us premise that the answer to this question is known experimentally to differ for many organisms and for many classes of characters, and may almost certainly be in part determined by external circumstances. But omitting the last qualification, certain principles are now clearly detected, though what principle will apply in any given case can only be determined by direct experiment made with that case.

This is the phenomenon of *cross*-breeding. As generally used, this term means the union of members of dissimilar varieties, or species: though when dissimilar gametes† produced by two individuals of the same variety unite in fertilisation, we have essentially *cross*-breeding in respect of the character or characters in which those gametes differ. We will suppose, as before, that these two gametes bearing properties unlike in respect of a given character, are borne by different individuals.

In the simplest case, suppose a gamete from an individual presenting any character in intensity A unite in fertilisation with another from an individual presenting the same character in intensity a. For brevity's sake we

* In all the cases discussed it is assumed that the gametes are similar except in regard to the "heritage" they bear, and that no *original* variation is taking place. The case of mosaics is also left wholly out of account (see later).

† The term "gamete" is now generally used as the equivalent of "germ-cell," whether male or female, and the term "zygote" is here used for brevity to denote the organism resulting from fertilisation.

may call the parent individuals A and a, and the resulting zygote Aa. What will the structure of Aa be in regard to the character we are considering?

Up to Mendel no one proposed to answer this question in any other way than by reference to the intensity of the character in the progenitors, and *primarily* in the parents, A and a, in whose bodies the gametes had been developed. It was well known that such a reference gave a very poor indication of what Aa would be. Both A and a may come from a population consisting of individuals manifesting the same character in various intensities. In the pedigree of either A or a these various intensities may have occurred few or many times. Common experience leads us to expect the probability in regard to Aa to be influenced by this history. The next step is that which Galton took. He extended the reference beyond the immediate parents of Aa, to its grandparents, great-grandparents, and so on, and in the cases he studied he found that from a knowledge of the intensity in which the given character was manifested in each progenitor, even for some few generations back, a fairly accurate prediction could be made, not as to the character of any individual Aa, but as to the average character of Aa's of similar parentage, in general.

But suppose that instead of individuals presenting one character in differing intensities, two individuals breed together distinguished by characters which we know to be mutually exclusive, such as A and B. Here again we may speak of the individuals producing the gametes as A and B, and the resulting zygote as AB. What will AB be like? The population here again may consist of many like A and like B. These two forms may have been breeding together indiscriminately, and there may have been many or few of either type in the pedigree of either A or B.

Here again Galton applied his method with remarkable success. Referring to the progenitors of A and B, determining how many of each type there were in the direct pedigree of A and of B, he arrived at the same formula as before, with the simple difference that instead of expressing the probable average intensity of one character in several individuals, the prediction is given in terms of the probable number of A's and B's that would result on an average when particular A's and B's of known pedigree breed together.

The law as Galton gives it is as follows :—

"It is that the two parents contribute between them on the average one-half, or (0·5) of the total heritage of the offspring; the four grandparents, one-quarter, or $(0{\cdot}5)^2$; the eight great-grandparents, one-eighth, or $(0{\cdot}5)^3$, and so on. Then the sum of the ancestral contributions is expressed by the series

$$\{(0{\cdot}5) + (0{\cdot}5)^2 + (0{\cdot}5)^3, \text{ \&c.}\},$$

which, being equal to 1, accounts for the whole heritage."

In the former case where A and a are characters which can be denoted by reference to a common scale, the law assumes of course that the inheritance will be, to use Galton's term, *blended,* namely that the zygote resulting from the union of A with a will on the average be more like a than if A had been united with A ; and conversely that an Aa zygote will on the average *be more like* A *than an* aa *zygote would be.*

But in the case of A's and B's, which are assumed to be mutually exclusive characters, we cannot speak of blending, but rather, to use Galton's term, of *alternative* inheritance.

Pearson, finding that the law whether formulated thus, or in the modified form in which he restated it*, did not express the phenomena of alternative inheritance known to him with sufficient accuracy to justify its strict application to them, and also on general grounds, proposed that the phenomena of blended and alternative inheritance should be treated apart—a suggestion† the wisdom of which can scarcely be questioned.

Now the law thus imperfectly set forth and every modification of it is incomplete in one respect. It deals only with the characters of the resulting zygotes and predicates nothing in regard to the gametes which go to form them. A good prediction may be made as to any given group of zygotes, but the various possible constitutions of the gametes are not explicitly treated.

Nevertheless a definite assumption is implicitly made regarding the gametes. It is not in question that differences between these gametes may occur in respect of the heritage they bear; yet it is assumed that these differences will be distributed among the gametes of any individual zygote in such a way that each gamete remains capable, on fertilisation, of transmitting *all* the characters (both of the parent-zygote and of its progenitors) to the zygote which it then contributes to form (and to the posterity of that zygote) in the intensity indicated by the law. Hence the gametes of any individual are taken as collectively a fair sample of all the racial characters in their appropriate intensities, and this theory demands that there shall have been no qualitative redistribution of characters among the gametes of any zygote in such a way that some gametes shall be finally excluded from partaking of and transmitting any specific

* In Pearson's modification the parents contribute 0·3, the grandparents 0·15, the great-grandparents ·075.

† See the works referred to above.

part of the heritage. The theory further demands—and by the analogy of what we know otherwise not only of animals and plants, but of physical or chemical laws, perhaps this is the most serious assumption of all—that the structure of the gametes shall admit of their being capable of transmitting any character in any intensity varying from zero to totality with equal ease; and that gametes of each intensity are all equally likely to occur, given a pedigree of appropriate arithmetical composition.

Such an assumption appears so improbable that even in cases where the facts seem as yet to point to this conclusion with exceptional clearness, as in the case of human stature, I cannot but feel there is still room for reserve of judgment.

However this may be, the Law of Ancestral Heredity, and all modifications of it yet proposed, falls short in the respect specified above, that *it does not directly attempt to give any account of the distribution of the heritage among the gametes* of any one individual.

Mendel's conception differs fundamentally from that involved in the Law of Ancestral Heredity. The relation of his hypothesis to the foregoing may be most easily shown if we consider it first in application to the phenomena resulting from the cross-breeding of two pure varieties.

Let us again consider the case of two varieties each displaying the same character, but in the respective intensities A and a. Each gamete of the A variety bears A, and each gamete of the a variety bears a. When they unite in fertilisation they form the zygote Aa. What will be its characters? The Mendelian teaching would reply that this can only be known by direct experiment with the two forms A and a, and that the characters A and a perceived in those two forms or varieties need not give any indication as to the character of the zygote Aa. It may display the character A, or a, or a character half way between the two, or a character beyond A or below a. The character of Aa is not regarded as a *heritage* transmitted to it by A and by a, but as a character special and peculiar to Aa, just as NaCl is not a body half way between sodium and chlorine, or such that its properties can be predicted from or easily stated in terms of theirs.

If a concrete case may help, a tall pea A crossed with a dwarf a often produces, not a plant having the height of either A or a, but something *taller* than the pure tall variety A.

But if the case obeys the Mendelian principles—as does that here quoted—then it can be declared *first* that the gametes of Aa will not be bearers of the character proper to Aa; but, generally speaking, each gamete will either bear the pure A character or the pure a character. There will in fact be a redistribution of the characters brought in by the gametes which united to form the zygote Aa, such that each gamete of Aa is pure, as the parental gametes were. *Secondly* this redistribution will occur in such a way that, of the gametes produced by such Aa's, on an average there will be equal numbers of A gametes and of a gametes.

Consequently if Aa's breed together, the new A gametes may meet each other in fertilisation, forming a zygote AA, namely, the pure A variety again; similarly two a gametes may meet and form aa, or the pure a variety again. But if an A gamete meets an a it will once more form Aa, with its special character. This Aa is the hybrid, or "mule" form, or as I have elsewhere called it, the *heterozygote*, as distinguished from AA or aa the *homozygotes*.

Similarly if the two gametes of two varieties distinguished by characters, A and B, which cannot be described in terms of any common scale (such as for example the "rose" and "single" combs of fowls) unite in fertilisation, again the character of the mule form cannot be predicted. Before the experiment is made the "mule" may present *any* form. Its character or properties can as yet be no more predicted than could those of the compounds of unknown elements before the discovery of the periodic law.

But again—if the case be Mendelian—the gametes borne by AB will be either A's or B's*, and the cross-bred AB's breeding together will form AA's, AB's and BB's. Moreover, if as in the normal Mendelian case, AB's bear on an average equal numbers of A gametes and B gametes, the numerical ratio of these resulting zygotes to each other will be

$$1\,AA : 2\,AB : 1\,BB.$$

We have seen that Mendel makes no prediction as to the outward and visible characters of AB, but only as to the essential constitution and statistical condition of its gametes in regard to the characters A and B. Nevertheless in a large number of cases the character of AB is known to fall into one of three categories (omitting mosaics).

(1) The cross-bred may almost always resemble one of its pure parents so closely as to be practically indistinguishable from that pure form, as in the case of the yellow cotyledon-colour of certain varieties of peas when crossed with green-cotyledoned varieties; in which case the parental character, yellow, thus

* This conception was clearly formed by Naudin simultaneously with Mendel, but it was not worked out by him and remained a mere suggestion. In one place also Focke came very near to the same idea (see Bibliography).

manifested by the cross-bred is called "dominant" and the parental character, green, not manifested, is called recessive.

(2) The cross-bred may present some condition intermediate between the two parental forms, in which case we may still retain the term "blend" as applied to the zygote.

Such an "intermediate" may be the apparent mean between the two parental forms or be nearer to one or other in any degree. Such a case is that of a cross between a rich crimson Magenta Chinese Primrose and a clear White, giving a flower of a colour appropriately described as a "washy" magenta.

(3) The cross-bred may present some form quite different from that of either pure parent. Though, as has been stated, nothing can be predicted of an unknown case, we already know a considerable number of examples of this nature in which the mule-form *approaches sometimes with great accuracy to that of a putative ancestor, near or remote.* It is scarcely possible to doubt that several—though perhaps not all—of Darwin's "reversions on crossing" were of this nature.

Such a case is that of the "wild grey mouse" produced by the union of an albino tame mouse and a piebald Japanese mouse*. These "reversionary" mice bred together produce the parental tame types, some other types, and "reversionary" mice again.

From what has been said it will now be clear that the applicability of the Mendelian hypothesis has, intrinsically,

* See von Guaita, *Ber. naturf. Ges. Freiburg* x. 1898 and xi. 1899, quoted by Professor Weldon (see later).

nothing whatever to do with the question of the inheritance being *blended* or *alternative.* In fact, as soon as the relation of zygote characters to gamete characters is appreciated, it is difficult to see any reason for supposing that the manifestation of characters seen in the zygotes should give any indication as to their mode of allotment among the gametes.

On a previous occasion I pointed out that the terms "Heredity" and "Inheritance" are founded on a misapplication of metaphor, and in the light of our present knowledge it is becoming clearer that the ideas of "transmission" of a character by parent to offspring, or of there being any "contribution" made by an ancestor to its posterity, must only be admitted under the strictest reserve, and merely as descriptive terms.

We are now presented with some entirely new conceptions :—

(1) The purity of the gametes in regard to certain characters.

(2) The distinction of all zygotes according as they are or are not formed by the union of like or unlike gametes. In the former case, apart from Variation, they breed true when mated with their like ; in the latter case their offspring, collectively, will be heterogeneous.

(3) If the zygote be formed by the union of dissimilar gametes, we may meet the phenomenon of (*a*) dominant and recessive characters ; (*b*) a blend form ; (*c*) a form distinct from either parent, often reversionary*.

* This fact sufficiently indicates the difficulties involved in a superficial treatment of the phenomenon of reversion. To call such reversions as those named above "returns to ancestral type" would be, if more than a descriptive phrase were intended, quite misleading.

But there are additional and even more significant deductions from the facts. We have seen that the gametes are differentiated in respect of pure characters. Of these pure characters there may *conceivably* be any number associated together in one organism. In the pea Mendel detected at least seven—not all seen by him combined in the same plant, but there is every likelihood that they are all capable of being thus combined.

Each such character, which is capable of being dissociated or replaced by its contrary, must henceforth be conceived of as a distinct *unit-character*; and as we know that the several unit-characters are of such a nature that any one of them is capable of independently displacing or being displaced by one or more alternative characters taken singly, we may recognize this fact by naming such unit-characters *allelomorphs*. So far, we know very little of any allelomorphs existing otherwise than as *pairs* of contraries, but this is probably merely due to experimental limitations and the rudimentary state of our knowledge.

In one case (combs of fowls) we know three characters, *pea* comb, *rose* comb and *single* comb; of which *pea* and *single*, or *rose* and *single*, behave towards each other as a pair of allelomorphs, but of the behaviour of *pea* and *rose* towards each other we know as yet nothing.

We have no reason as yet for affirming that any phenomenon properly described as *displacement* of one allelomorph by another occurs, though the metaphor may be a useful one. In all cases where *dominance* has been perceived, we can affirm that the members of the allelomorphic pair stand to each other in a relation the nature

It is not the ancestral *type* that has come back, but something else has come in its guise, as the offspring presently prove. For the first time we thus begin to get a rationale of "reversion."

of which we are as yet wholly unable to apprehend or illustrate.

To the new conceptions already enumerated we may therefore add

(4) *Unit-characters* of which some, *when once arisen by Variation*, are alternative to each other in the constitution of the gametes, according to a definite system.

From the relations subsisting between these characters, it follows that as each zygotic union of allelomorphs is *resolved* on the formation of the gametes, no zygote can give rise to gametes collectively representing more than *two* characters allelomorphic to each other, apart from new variation.

From the fact of the existence of the interchangeable characters we must, for purposes of treatment, and to complete the possibilities, necessarily form the conception of an *irresoluble base*, though whether such a conception has any objective reality we have no means as yet of determining.

We have now seen that when the varieties A and B are crossed together, the heterozygote, AB, produces gametes bearing the pure A character and the pure B character. In such a case we speak of such characters as *simple* allelomorphs. In many cases however a more complex phenomenon happens. The character brought in on fertilisation by one or other parent may be of such a nature that when the zygote, AB, forms its gametes, these are not individually bearers merely of A and B, *but of a number of characters themselves again integral*, which in, say A, behaved as one character so long as its gametes united in fertilisation with others like themselves, but on cross-fertilisation are resolved and redistributed among the gametes produced by the cross-bred zygote.

In such a case we call the character A a *compound* allelomorph, and we can speak of the integral characters which constitute it as *hypallelomorphs*. We ought to write the heterozygote $(AA'A''...)\ B$ and the gametes produced by it may be of the form A, A', A'', A''',...B. Or the resolution may be incomplete in various degrees, as we already suspect from certain instances; in which case we may have gametes A, $A'A''$, $A'''A''''$, $A'A''A^{v}$,...B, and so on. Each of these may meet a similar or a dissimilar gamete in fertilisation, forming either a homozygote, or a heterozygote with its distinct properties.

In the case of compound allelomorphs we know as yet nothing of the statistical relations of the several gametes.

Thus we have the conception

(5) *of a Compound character*, borne by one gamete, transmitted entire as a single character so long as fertilisation only occurs between like gametes, or is, in other words, "symmetrical," but if fertilisation take place with a dissimilar gamete (or possibly by other causes), resolved into integral constituent-characters, each separately transmissible.

Next, as, by the union of the gametes bearing the various hypallelomorphs with other such gametes, or with gametes bearing simple allelomorphs, in fertilisation, a number of new zygotes will be formed, such as may not have been seen before in the breed: these will inevitably be spoken of as *varieties*; and it is difficult not to extend the idea of variation to them. To distinguish these from other variations—which there must surely be—we may call them

(6) *Analytical* variations in contradistinction to

(7) *Synthetical* variations, occurring not by the separation of pre-existing constituent-characters but by the addition of new characters.

Lastly, it is impossible to be presented with the fact that in Mendelian cases the cross-bred produces on an average *equal* numbers of gametes of each kind, that is to say, a symmetrical result, without suspecting that this fact must correspond with some symmetrical figure of distribution of those gametes in the cell-divisions by which they are produced.

At the present time these are the main conceptions—though by no means all—arising directly from Mendel's work. The first six are all more or less clearly embodied by him, though not in every case developed in accordance with modern knowledge. The seventh is not a Mendelian conception, but the facts before us justify its inclusion in the above list though for the present it is little more than a mere surmise.

In Mendelian cases it will now be perceived that all the zygotes composing the population consist of a limited number of possible types, each of definite constitution, bearing gametes also of a limited and definite number of types, and definite constitution in respect of pre-existing characters. It is now evident that in such cases each several progenitor need not be brought to account in reckoning the probable characters of each descendant; for the gametes of cross-breds are differentiated at each successive generation, some parental (Mendelian) characters being left out in the composition of each gamete produced by a zygote arising by the union of bearers of opposite allelomorphs.

When from these considerations we return to the phenomena comprised in the Law of Ancestral Heredity, what certainty have we that the same conceptions are not applicable there also?

It has now been shown that the question whether in the cross-bred zygotes in general the characters blend or are mutually exclusive is an entirely subordinate one, and distinctions with regard to the essential nature of heredity based on these circumstances become irrelevant.

In the case of a population presenting continuous variation in regard to say, stature, it is easy to see how purity of the gametes in respect of any intensities of that character might not in ordinary circumstances be capable of detection. There are doubtless more than two pure gametic forms of this character, but there may quite conceivably be six or eight. When it is remembered that each heterozygous combination of any two may have its own appropriate stature, and that such a character is distinctly dependent on external conditions, the mere fact that the observed curves of stature give "chance distributions" is not surprising and may still be compatible with purity of gametes in respect of certain pure types. In peas (*P. sativum*), for example, from Mendel's work we know that the tall forms and the extreme dwarf forms exhibit gametic purity. I have seen at Messrs Sutton's strong evidence of the same nature in the case of the tall Sweet Pea (*Lathyrus odoratus*) and the dwarf or procumbent "Cupid" form.

But in the case of the Sweet Pea we know at least one pure form of definitely intermediate height, and in the case of *P. sativum* there are many. When the *extreme* types breed together it will be remembered the heterozygote commonly exceeds the taller in height. In the next generation, since there is, in the case of extremes, so much margin between the types of the two pure forms, the return of the offspring to the three forms of which two are homozygous and one heterozygous is clearly perceptible.

If however instead of pure extreme varieties we were to take a pair of varieties differing normally by only a foot or two, we might, owing to the masking effects of conditions, &c., have great difficulty in distinguishing the three forms in the second generation. There would besides be twice as many heterozygous individuals as homozygous individuals of each kind, giving a symmetrical distribution of heights, and who might not—in pre-Mendelian days—have accepted such evidence—made still less clear by influence of conditions—as proof of Continuous Variation both of zygotes and gametes?

Suppose, then, that instead of two pure types, we had six or eight breeding together, each pair forming their own heterozygote, there would be a very remote chance of such purity or fixity of type whether of gamete or zygote being detected.

Dominance, as we have seen, is merely a phenomenon incidental to specific cases, between which no other common property has yet been perceived. In the phenomena of *blended* inheritance we clearly have no dominance. In the cases of *alternative* inheritance studied by Galton and Pearson there is evidently no *universal* dominance. From the tables of Basset hound pedigrees there is clearly no definite dominance of either of the coat-colours. In the case of eye-colour the published tables do not, so far as I have discovered, furnish the material for a decision, though it is scarcely possible the phenomenon, even if only occasional, could have been overlooked. We must take it, then, there is no sensible dominance in these cases; but whether there is or is not sensible gametic purity is an altogether different question, which, so far as I can judge, is as yet untouched. It may perfectly well be that we shall be compelled to recognize that in many cases there is no such purity, and that the characters may be carried by the gametes in any proportion from zero to totality, just as some substances may be carried in a solution in any proportion from zero to saturation without discontinuous change of properties. That this will be found true in *some* cases is, on any hypothesis, certain; but to prove the fact for any given case will be an exceedingly difficult operation, and I scarcely think it has been yet carried through in such a way as to leave no room for doubt.

Conversely, the *absolute* and *universal* purity of the gametes has certainly not yet been determined for any case; not even in those cases where it looks most likely that such universal purity exists. Impairment of such purity we may conceive either to occur in the form of mosaic gametes, or of gametes with blended properties. On analogy and from direct evidence we have every right to believe that gametes of both these classes may occur in rare and exceptional cases, of as yet unexplored nature*, but such a phenomenon will not diminish the significance of observed purity.

We have now seen the essential nature of the Mendelian principles and are able to appreciate the exact relation in which they stand to the group of cases included in the Law of Ancestral Heredity. In seeking any general indication as to the common properties of the phenomena which are already known to obey Mendelian principles we can as yet point to none, and whether some such common features exist or not is unknown.

There is however one group of cases, definite though as yet not numerous, where we know that the Mendelian

* It will be understood from what follows, that the existence of mosaic zygotes is no *proof* that either component gamete was mosaic.

principles do not apply. These are the phenomena upon which Mendel touches in his brief paper on *Hieracium*. As he there states, the hybrids, if they are fertile at all, produce offspring like themselves, not like their parents. In further illustration of this phenomenon he cites Wichura's *Salix* hybrids. Perhaps some dozen other such illustrations could be given which rest on good evidence. To these cases the Mendelian principle will in nowise apply, nor is it easy to conceive any modification of the law of ancestral heredity which can express them. There the matter at present rests. Among these cases, however, we perceive several more or less common features. They are often, though not always, hybrids between forms differing in many characters. The first cross frequently is not the exact intermediate between the two parental types, but may as in the few *Hieracium* cases be irregular in this respect. There is often some degree of sterility. In the absence of fuller and statistical knowledge of such cases further discussion is impossible.

Another class of cases, untouched by any hypothesis of heredity yet propounded, is that of the false hybrids of Millardet, where we have fertilisation without transmission of one or several parental characters. In these not only does the first cross show, in some respect, the character or characters of *one parent only*, but in its posterity *no reappearance of the lost character or characters is observed.* The nature of such cases is still quite obscure, but we have to suppose that the allelomorph of one gamete only developes after fertilisation to the exclusion of the corresponding allelomorph of the other gamete, much—if the crudity of the comparison may be pardoned—as occurs on the female side in parthenogenesis without fertilisation at all.

To these as yet altogether unconformable cases we can scarcely doubt that further experiment will add many more. Indeed we already have tolerably clear evidence that many phenomena of inheritance are of a much higher order of complexity. When the paper on *Pisum* was written Mendel apparently inclined to the view that with modifications his law might be found to include all the phenomena of hybridisation, but in the brief subsequent paper on *Hieracium* he clearly recognized the existence of cases of a different nature. Those who read that contribution will be interested to see that he lays down a principle which may be extended from hybridisation to heredity in general, that the laws of each new case must be determined by separate experiment.

As regards the Mendelian principles, which it is the chief aim of this introduction to present clearly before the reader, a professed student of variation will easily be able to fill in the outline now indicated, and to illustrate the various conceptions from phenomena already familiar. To do this is beyond the scope of this short sketch. But enough perhaps has now been said to show that by the application of those principles we are enabled to reach and deal in a comprehensive manner with phenomena of a fundamental nature, lying at the very root of all conceptions not merely of the physiology of reproduction and heredity, but even of the essential nature of living organisms; and I think that I used no extravagant words when, in introducing Mendel's work to the notice of readers of the Royal Horticultural Society's Journal, I ventured to declare that his experiments are worthy to rank with those which laid the foundation of the Atomic laws of Chemistry.

As some biographical particulars of this remarkable investigator will be welcome, I give the following brief notice, first published by Dr Correns on the authority of Dr von Schanz: Gregor Johann Mendel was born on July 22, 1822, at Heinzendorf bei Odrau, in Austrian Silesia. He was the son of well-to-do peasants. In 1843 he entered as a novice the "Königinkloster," an Augustinian foundation in Altbrünn. In 1847 he was ordained priest. From 1851 to 1853 he studied physics and natural science at Vienna. Thence he returned to his cloister and became a teacher in the Realschule at Brünn. Subsequently he was made Abbot, and died January 6, 1884. The experiments described in his papers were carried out in the garden of his Cloister. Besides the two papers on hybridisation, dealing respectively with *Pisum* and *Hieracium*, Mendel contributed two brief notes to the *Verh. Zool. bot. Verein*, Wien, on *Scopolia margaritalis* (1853, III., p. 116) and on *Bruchus pisi* (*ibid.* 1854, IV., p. 27). In these papers he speaks of himself as a pupil of Kollar.

Mendel published in the Brünn journal statistical observations of a meteorological character, but, so far as I am aware, no others relating to natural history. Dr Correns tells me that in the latter part of his life he engaged in the Ultramontane Controversy. He was for a time President of the Brünn Society*.

For the photograph of Mendel which forms the frontispiece to this work, I am indebted to the Very Rev. Dr Janeischek, the present Abbot of Brünn, who most kindly supplied it for this purpose.

So far as I have discovered there was, up to 1900, only one reference to Mendel's observations in scientific literature, namely that of Focke, *Pflanzenmischlinge*, 1881, p. 109,

* A few additional particulars are given in Tschermak's edition.

where it is simply stated that Mendel's numerous experiments on *Pisum* gave results similar to those obtained by Knight, but that he believed he had found constant numerical ratios among the types produced by hybridisation. In the same work a similar brief reference is made to the paper on *Hieracium*.

It may seem surprising that a work of such importance should so long have failed to find recognition and to become current in the world of science. It is true that the journal in which it appeared is scarce, but this circumstance has seldom long delayed general recognition. The cause is unquestionably to be found in that neglect of the experimental study of the problem of Species which supervened on the general acceptance of the Darwinian doctrines. The problem of Species, as Kölreuter, Gärtner, Naudin, Wichura, and the other hybridists of the middle of the nineteenth century conceived it, attracted thenceforth no workers. The question, it was imagined, had been answered and the debate ended. No one felt much interest in the matter. A host of other lines of work were suddenly opened up, and in 1865 the more original investigators naturally found those new methods of research more attractive than the tedious observations of the hybridisers, whose inquiries were supposed, moreover, to have led to no definite result.

Nevertheless the total neglect of such a discovery is not easy to account for. Those who are acquainted with the literature of this branch of inquiry will know that the French Academy offered a prize in 1861 to be awarded in 1862 on the subject "*Étudier les Hybrides végétaux au point de vue de leur fécondité et de la perpétuité de leurs caractères.*" This subject was doubtless chosen with reference to the experiments of Godron of Nancy and Naudin, then of Paris. Both these naturalists competed, and the accounts of the work of Godron on *Datura* and of Naudin on a number of species were published in the years 1864 and 1865 respectively. Both, especially the latter, are works of high consequence in the history of the science of heredity. In the latter paper Naudin clearly enuntiated what we shall henceforth know as the Mendelian conception of the dissociation of characters of cross-breds in the formation of the germ-cells, though apparently he never developed this conception.

In the year 1864, George Bentham, then President of the Linnean Society, took these treatises as the subject of his address to the Anniversary meeting on the 24 May, Naudin's work being known to him from an abstract, the full paper having not yet appeared. Referring to the hypothesis of dissociation which he fully described, he said that it appeared to be new and well supported, but required much more confirmation before it could be held as proven. (*J. Linn. Soc.*, *Bot.*, VIII., *Proc.*, p. XIV.)

In 1865, the year of Mendel's communication to the Brünn Society, appeared Wichura's famous treatise on his experiments with *Salix* to which Mendel refers. There are passages in this memoir which come very near Mendel's principles, but it is evident from the plan of his experiments that Mendel had conceived the whole of his ideas before that date.

In 1868 appeared the first edition of Darwin's *Animals and Plants*, marking the very zenith of these studies, and thenceforth the decline in the experimental investigation of Evolution and the problem of Species has been steady. With the rediscovery and confirmation of Mendel's work by de Vries, Correns and Tschermak in 1900 a new era begins.

That Mendel's work, appearing as it did, at a moment when several naturalists of the first rank were still occupied with these problems, should have passed wholly unnoticed, will always remain inexplicable, the more so as the Brünn Society exchanged its publications with most of the Academies of Europe, including both the Royal and Linnean Societies.

Naudin's views were well known to Darwin and are discussed in *Animals and Plants* (ed. 1885, II., p. 23); but, put forward as they were without full proof, they could not command universal credence. Gärtner, too, had adopted opposite views; and Wichura, working with cases of another order, had proved the fact that some hybrids breed true. Consequently it is not to be wondered at that Darwin was sceptical. Moreover, the Mendelian idea of the "hybrid-character," or heterozygous form, was unknown to him, a conception without which the hypothesis of dissociation of characters is quite imperfect.

Had Mendel's work come into the hands of Darwin, it is not too much to say that the history of the development of evolutionary philosophy would have been very different from that which we have witnessed.